UNIVERSIDADE FEDERAL DE SERGIPE

PRÓ-REITORIA DE PÓS-GRADUAÇÃO E PESQUISA

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E CONSERVAÇÃO

EFEITOS DOS PROCESSOS BIÓTICOS E ABIÓTICOS NA DIVERSIFICAÇÃO DOS NEOSELACHII

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SÃO CRISTÓVÃO, SE

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia e Conservação da Universidade Federal de Sergipe, como parte dos requisitos necessários para a obtenção do título de Mestre em Ecologia e Conservação.

Orientador: Dr. Pablo Ariel Martinez
Co orientador: Dr. Anderson Aires Eduardo

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FICHA CATALOGRÁFICA ELABORADA PELA BIBLIOTECA CENTRAL
UNIVERSIDADE FEDERAL DE SERGIPE

Fernandes, Elisa Cravo
F363e Efeitos dos processos bióticos e abióticos na diversificação dos neoselacchii / Elisa Cravo Fernandes; orientadora Pablo Ariel Martinez. – São Cristóvão, SE, 2019.
68 f.: il.

Dissertação (mestrado em Ecologia e Conservação)– Universidade Federal de Sergipe, 2019.

1. Ecologia animal. 2. Tubarão (Peixe). 3. Arraia (Peixe). 4. Animais - Extinção. 5. Nicho (Ecologia). I. Martinez, Pablo Ariel, orient. II. Título.

CDU 591.522

TERMO DE APROVAÇÃO

Efeito dos Processos Bióticos e Abióticos na Diversificação dos Neoselachii

por

ELISA CRAVO FERNANDES

Dissertação apresentada ao Programa de Pós-Graduação em Ecologia e Conservação da Universidade Federal de Sergipe, como parte dos requisitos exigidos para a obtenção do título de Mestre em Ecologia e Conservação.

APROVADA pela banca examinadora composta por

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São Cristóvão/SE, 28 de fevereiro de 2019

Dedico esta dissertação a todo aquele

que faz da pesquisa seu ofício.

AGRADECIMENTOS

"*If I have seen further it is by standing on the shoulders of Giants.*"

– Isaac Newton

Gostaria de agradecer a todos aqueles que de alguma forma contribuíram para a concretização dessa dissertação.

Em primeiro lugar, gostaria de agradecer à Deus, meu Salvador, por ser meu alimento dia e noite e me sustentar durante todo o processo.

Em segundo lugar, gostaria de agradecer aos meus orientadores Dr. Pablo Ariel Martinez e Dr. Anderson Aires Eduardo, por embarcarem junto comigo nessa jornada e me oferecerem todo suporte necessário. Obrigada pelos ensinamentos, puxões de orelhas e incentivos.

Gostaria de agradecer também ao professor Dr. Alexandre Liparini, do Laboratório de Paleontologia, por todo suporte com a análise evolutiva do projeto. Vida longa aos fósseis.

Gostaria de agradecer aos pesquisadores Dra. Maria Lúcia Goes de Araújo, Dr. Davi Mello Crescente, Dr. Gustavo Burin e Dr. Mário André Trindade Dantas, que fizeram parte das minhas bancas e cujas recomendações foram incorporadas à versão final desta dissertação. Obrigada pelas contribuições.

Aos colegas de laboratórios do Laboratório de Pesquisas Integrativas em Biodiversidade (PIBi Lap) e do Laboratório de Paleontologia (em especial Fran e Will) por dividirem comigo as dores e delícias da vida acadêmica e por tornarem o laboratório um ambiente acolhedor... e pelo café nosso de cada dia.

Aos colegas e professores do programa de de pós-graduação em Ecologia e Conservação, em especial à minha turma (2017) por todo companheirismo e cumplicidade ao longo desses dois anos. E aproveito para fazer um agradecimento especial à Juliana Cordeiro, secretária do programa, por todo empenho e prestatividade.

À Universidade Federal de Sergipe, que foi minha casa nos últimos anos, por toda estrutura oferecida, apesar do sucateamento das universidades. Obrigada por permanecer firme. À Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) pelo fomento da bolsa de pesquisa.

À Alexandra Elbakyan por quebrar as barreiras da ciência, tornando-a acessível a todos.

Por fim, gostaria de agradecer à minha família, meus pais e irmãos (e Chiquinha), por me apoiarem e me darem o suporte necessário. Aos meus irmãos em Cristo, Grazi, Emilly, Kézia, Daniel e Dinah, por torcerem sempre por mim e me ampararem quando preciso. Aos meus amigos Mai, Joice, Iére, Dany, Liz, Rauber, Paulinho, Vini, Carol, por todo apoio e compreensão.

E por último, gostaria de agradecer a mim mesma, por toda perseverança e autocontrole...

SUMÁRIO

Where the fin of the shark cuts like a black chip out of the water...

— “Song of Myself”, Walt Whitman

RESUMO

Eventos de extinções e substituição de espécies são onipresentes na história evolutiva do planeta, sendo conduzidos por fatores bióticos e abióticos. O conhecimento sobre padrões evolutivos no ambiente marinho ainda é escasso, uma vez que a maior parte dos estudos é realizado no ambiente terrestre. Os Neoselachii, clado que se originou no período Carbonífero e enfrentou sua maior diversificação durante o Jurássico-Cretáceo, enfrentaram as três últimas grandes extinções. Nesse trabalho analisamos as taxas de especiação, extinção e diversificação para tubarões e raias a fim de avaliar se e como as três últimas extinções em massa influenciaram na diversificação do grupo aqui estudado a nível de clado e de ordem. Também avaliamos se mudanças ambientais e interações ecológicas afetaram as taxas de extinção das ordens de Neoselachii. Nossos resultados mostram que as extinções em massa não exerceram influência sobre as taxas de diversificação do grupo. Entretanto observou-se um aumento na taxa de extinção no final do Mioceno, coincidindo com eventos de extinções de fundo que ocorreram na época. Os dados obtidos através da análise de diversificação foram associados às alterações ambientais do período em questão e à diversificação de grupos potencialmente competitivos – Delphinidae (Mammals: Odontoceti). Nós encontramos que a diminuição da temperatura e as oscilações do nível do mar provocaram um aumento nas taxas de extinção das ordens analisadas. Nossos resultados também indicam que a competição intraclado e intercalado influenciou negativamente as taxas de extinção. Entender como os fatores bióticos e abióticos afetam os organismos fornece informações importantes sobre a biodiversidade atual e sobre as consequências de futuros eventos que podem ocorrer. Portanto, o estudo de organismos extintos e atuais auxilia na predição de impactos de futuras mudanças ambientais. Sendo assim, espera-se que os resultados aqui apresentados ofereçam uma base para futuros estudos que permitam predizer como esse grupo reagirá em caso de novas extinções em massa.

Palavras chave: competição, extinção, nível do mar, PyRate, raia, temperatura, tubarão

ABSTRACT

Events of extinctions and species replacement are ubiquitous in the Earth's evolutionary history, being driven by biotic and abiotic factors. Knowledge about evolutionary patterns in the marine environment is still scarce, since most studies are conducted in the terrestrial environment. The Neoselachii, clade which originated in the Carboniferous period and experimented its greater diversification during the Jurassic-Cretaceous, faced the last three great extinctions. In this work we analyse the species speciation, extinction and diversification rates for sharks and rays in order to evaluate if and how the last three mass extinctions influenced the Neoselachii diversification at clade and order level. We also evaluated whether environmental changes and ecological interactions affected the extinction rates of Neoselachii orders. Our results showed that mass extinctions did not influence the diversification rates of the group. However, there was an increase in the extinction rate at the end of the Miocene, coinciding with events of background extinctions that occurred at this time. The data obtained through the diversification analysis were associated with environmental changes of the Miocene period and the diversification of putative competitive groups - Delphinidae (Mammals: Odontoceti). We found that decrease in temperature and sea level oscillations caused an increase in the extinction rates of the analyzed orders. Our results also indicate that intraclass and intercalated competition negatively influenced extinction rates. Understanding how biotic and abiotic factors affect organisms provides important information about current biodiversity and the consequences of future events that may occur. Therefore, the study of extinct and current organisms assists in the prediction of impacts of future environmental changes. Thus, it is expected that the results presented here will provide a basis for a possible prediction of how this group will react in extinctions future events.

Key words: competition, extinction, PyRate, ray, temperature, sea level, shark

INTRODUÇÃO GERAL

A diversificação de uma linhagem pode ser definida como um balanço entre suas taxas especiação e a extinção (Morlon, 2014; Pyron e Burbrink, 2013). As dinâmicas de diversificação são conduzidas por processos estocásticos, atributos intraespecíficos, complexidade geográfica e fatores ambientais (Ricklefs, 2007), determinando assim os padrões de biodiversidade observados. A substituição de espécies, ocasionada por sucessivos eventos de especiação e extinção, está presente em toda a história evolutiva do planeta. A perda de espécies é comum e esperada dentro de uma linhagem (extinções de fundo), entretanto alguns eventos catastróficos podem ocorrer a nível global (extinções em massa) (Benton, 2011), geralmente ocasionados por abruptas mudanças climáticas (Twitchett, 2006). Embora o ambiente marinho seja pouco estudado em relação ao ambiente terrestre, e os grupos marinhos sejam considerados menos susceptíveis à extinção (Dulvy, Sadovy e Reynolds, 2003), eventos de extinções estão presentes no registro fóssil marinho (Alroy, 2008; Peters, 2008), sendo as alterações no nível do mar e a temperatura as causas mais relacionadas a essas extinções. Apesar da diversificação ser amplamente associada a fatores abióticos, as interações ecológicas também exercem influência nas suas dinâmicas, em particular a competição (Benton, 2009; Valkenburgh, 2007). As interações competitivas podem ser tanto a nível intraespecífico quanto a nível interespecífico, sendo mais comum entre espécies próximas filogeneticamente. Porém, a competição também ocorre entre espécies filogeneticamente distantes, sendo as similaridades ecológicas ou morfológicas as responsáveis por tal interação (Valkenburgh, 1999).

Devido às suas características ecológicas e evolutivas, os Chondrichthyes são considerados um grupo chave no estudo dos efeitos de fatores bióticos e abióticos na biodiversidade no ambiente marinho. A classe Condrictes compreende os peixes cartilaginosos e surgiu há aproximadamente 400 Ma (Benton *et al*., 2009). Subdivide-se em duas subclasses, Holocephali, clado composto pelas quimeras, e Elasmobranchii, que inclui os tubarões (Selachimorpha) e as raias (Batoidea) (Inoue *et al.,* 2010). Os Neoselachii, clado primitivo que deu origem aos tubarões e raias atuais, é o grupo mais diverso entre os condrictes, com dezesseis ordens distintas (Weigmann, 2016; fossilworks.org), possuindo representantes tanto fósseis como atuais. Ademais, possuem uma ampla distribuição geográfica, com espécies de superfície e zonas abissais (Wilga e Lauder, 2004). Os registros fósseis mais antigos reportam a origem do grupo no período

Carbonífero (358 Ma) (Duffin e Ward, 1983; Gunnell, 1933), apresentando duas possíveis fases de diversificação, uma no período Jurássico (201 Ma), causada por um evento de colonização com surgimento de novas ordens (Underwood, 2006), e uma segunda fase no período Cretáceo (66 Ma), ocasionada por modificações corporais e na morfologia dentária que permitiram a colonização dos mais variados ambientes (Underwood, 2006). Os Neoselachii apresentam uma variedade de formas corporais, desde corpos fusiformes até achatados (Fig. 1) (Wilga e Lauder, 2004), com algumas ordens apresentando gigantismo (Pimiento *et al.*, 2019) . A maioria das ordens apresentam a ectotermia como estratégia de termorregulação (Pimiento *et al.*, 2019; Wilga e Lauder, 2004), embora a mesotermia também esteja presente (Pimiento *et al.*, 2019). Possuem uma variedade de hábitos alimentares que podem ser agrupados em dois grandes grupos: macropredadores e filtradores (Pimiento *et al.*, 2019). Devido a essa gama de características morfológicas e ecológicas e a sua ampla distribuição geográfica, alterações climáticas e interações ecológicas exercem influência na sua diversificação.

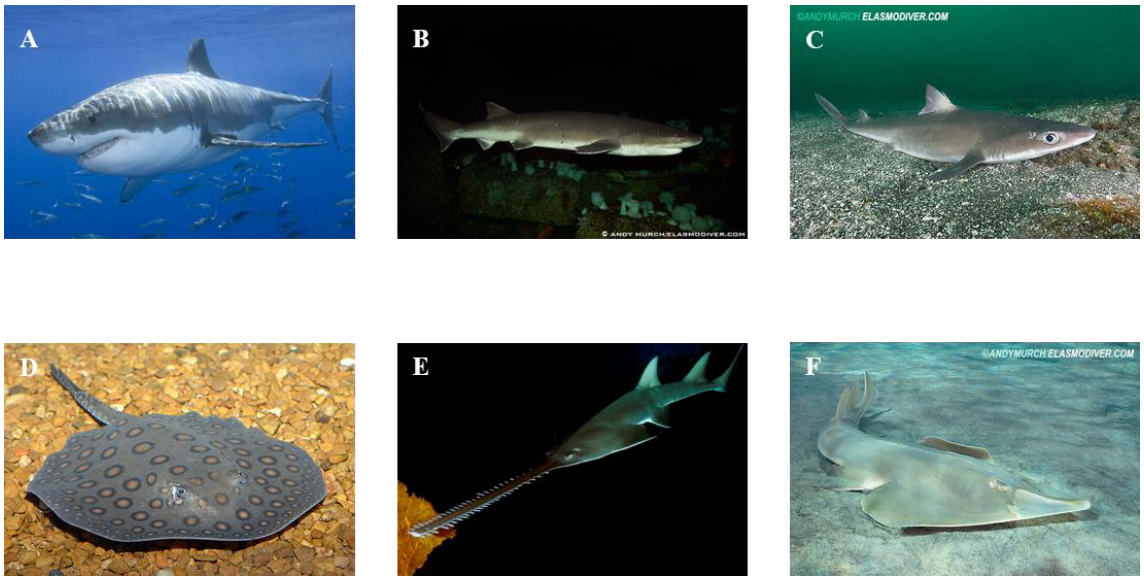

Figura 1. Representantes de Neoselachii com forma corporal fusiforme: (A) Lamniformes (*Carcharodon carcharias*), (B) Hexanchiformes (*Notorynchus cepedianus*), (C) Squaliformes (*Squalus japonicus*). Representantes de Neoselachii com forma corporal achatada: (D) Myliobatiformes (*Potamotrygon motoro*), (E) Pristiformes (*Pristis zijsron*), (F) Rhinobatiformes (*Glaucostegus halavi*). Fonte: Andy Murch – Elasmodiver (http://www.elasmodiver.com/sharks_and_rays.html).

Essa dissertação teve como objetivo avaliar qual o papel dos fatores bióticos e abióticos na diversificação dos Neoselachii a nível de clado e ordem, através de análises de inferência Bayesiana. No capítulo I analisamos se as grandes extinções influenciaram a diversificação (extinção e espciação) dos Neoselachii e das ordens. No capítulo II avaliamos os efeitos das mudanças de temperatura, alterações no nível do mar e competição intraclado e intercalado na diversificação do grupo a nível de ordem.

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Extinction is the rule. Survival is the exception.

— Carl Sagan

CHAPTER I - Neoselachii diversification: a group indifferent to the Mass Extinctions

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ABSTRACT

Neoselachii arose about 358 Mya, and faced the last three mass extinctions. In this work we analyse origination, extinction and diversification rates from different orders of sharks and rays. Our results show that the observed diversification patterns are not related to the incidence of mass extinctions. Moreover, there was an increase in extinction rate during the Paleogene period, coinciding with smaller scale extinction events at that time. We observed that the increase in extinction rate occurred in a phase of cooling of the Earth's surface and cetacean dispersion. The results presented here provide an insight into the factors outside the large extinctions which affected Neoselachii macroevolution and may still be operating today.

Key words: fossil records – PyRate – sharks – origination – rays

INTRODUCTION

Understanding the processes that drive changes in biodiversity patterns is a longstanding issue in paleoecological studies. To understand how biodiversity varies over time (Ezard *et al.*, 2011) and space (Rolland *et al.*, 2014; Rabosky *et al.*, 2018) it is necessary to identify the factors that modulate lineage diversification. Diversification can be defined as a balance between speciation and extinction rates (Pyron & Burbrink, 2013; Morlon, 2014) and is the key process in macroevolution studies (Morlon *et al*., 2010). This is a complex phenomenon, but it is widely accepted that factors like geographical complexity, intraspecific attributes (e.g., body size), dynamics of environmental conditions and stochastic processes influence the diversification rate (Ricklefs, 2007). Despite its central role in our understanding of biodiversity, the study of diversification is challenging, since speciation and extinction processes occur on a scale of millions of years (Morlon, 2014). Due to this difficulty, some methodologies have been developed in the study of diversification (Nee *et al.*, 1994), like diversification estimates using the fossil record, based on Bayesian approaches.

Earth's biodiversity is shaped by successive events of speciation and extinction. Species are constantly extinguished, while new ones arise, usually in local events. Thus, there is a natural loss of species over time, conventionally known as the background extinction rate (Benton, 2011). When catastrophic extinction events occur at global levels, causing the extinction of a large number of species independently to taxonomic groups and environments (e.g., marine and terrestrial) and in a short geological time, they are conventionally called mass extinctions (Benton, 2011). Among events with the highest extinction rates, five are considered mass extinctions due to the pervasive loss of biodiversity that they caused: Neordovician (443 Mya) (Sutcliffe *et al.*, 2000), Neodevonian (359 Mya) (Bambach, 2006), Perm-Triassic (251 Mya) (Knoll *et al.*, 2007),

Neotriassic (200 Mya) (Hesselbo *et al*., 2007) and Cretaceous-Paleogene (66 Mya) (Archibald *et al.*, 2010). Specific drivers of mass extinctions remain under debate, but climatic events are a common factor to all theories (Twitchett, 2006). The main cause of first great extinction, in the late Ordovician period, was the planet cooling after a glaciation period (Finney *et al.*, 1999; Wake & Vredenburg, 2008). Devonian extinction is related to an event of global anoxia in the oceans (Bond & Wignall, 2008). Permian extinction caused by volcanic eruptions, which caused the disappearance of two large structural ecosystems, corals and forests, leading to the extinction of between 80% and 90% of terrestrial and marine species (Benton, 2011). Volcanic activity and global warming are pointed out as the main causes of extinction at the end of Triassic period (Pálfy *et al.*, 2001; Hesselbo *et al.*, 2002). The researchers attribute two theories to explain the great extinction of Cretaceous: the most accepted postulates that an asteroid collided with Earth, while the other theory claims that large volcanic eruptions were responsible for the climate change that the planet experienced during the end of this period (Hallam & Wignall, 1999).

In general, marine species are considered less susceptible to extinction than terrestrial species (Dulvy et al., 2003). However, extinctions are ubiquitous in the marine fossil record (Alroy, 2008; Peters, 2008). Raup & Sepkosk (1982), estimated extinction rates of marine families every one million years, from fossil records, for four of the five mass extinctions: Ordovician (19.3 extinct families per million years), Permian (between 14 and 15.7 families), Triassic (10.8 families) and Cretaceous (16.3 families). Extinctions, both globally and locally, have a wide impact on the ecological structure, resilience, and resistance of ecosystem functions in marine environments (Worm *et al.*, 2006; Lotze *et al*., 2011). Understanding how mass extinction events affect organisms can provide critical information to understand the biodiversity we observe at present, as

well as consequences of impacts caused by events that may occur (Harnik *et al.*, 2012). The study of fossil records allows us to understand the evolutionary history of a clade, to reconstruct the paleoenvironment, to estimate the relative date of geological strata and to reconstitute Earth geological history (Cassab, 2010). Thus, the study of extinct and extant marine organism species helps to understand and predict present and future environmental changes impacts on the probability of extinction in the oceans. Even so, our understanding about how major extinction events shaped marine biodiversity remains widely unappreciated.

Neoselachii, the clade that gave rise to the current species of sharks and rays, is a key group to help us understand how large extinctions have affected biodiversity in the marine environment. First, the Neoselachii are the most diverse group within the Chondrichthyes (sixteen orders), having conquered all of the oceans, with surface and abyssal species existing. Also, it presents both extinct and extant lineages. Some fossil records of teeth indicate that the group originated in the Carboniferous period (358 Mya) (Duffin & Ward, 1983; Gunnell, 1933); however, the greatest diversity is observed in the Jurassic-Cretaceous period (201 Mya-66 Mya) (Benton, 2005; Underwood, 2006). Focusing on descriptive studies, some authors suggest that there have been two phases to the increase in the diversification of the clade. The first was a significant diversification in the Early Jurassic and probably in the Middle Jurassic, which is considered an ecological diversification, as it was possibly caused by a colonisation event, not a radiation event, and led to the first emergence of new orders (Underwood, 2006). This trend in diversity can be considered an "opportunistic" radiation event instead of a "competitive" one, as evolutionary innovations have allowed a better response of the group to perturbations of the environment and a better use of resources (Kriwet *et al.*, 2009). The second phase was larger and occurred through the Mid to Late Cretaceous

period; it was possibly driven by the evolutionary key innovations of the group related to modifications of the body plan and tooth morphology, which allowed the colonisation of a wide range of environments (Underwood, 2006). In addition, the feeding ecology (prey availability), associated with dental morphology, and trophic cascades also contributed to the Cretaceous diversification of the group (Bazzi *et al.*, 2018), once trophic cascades affect lower trophic levels which indirectly affect higher trophic levels. Because they have a cartilaginous skeleton, Elasmobranchii fossil records are poor and composed mostly of scales and isolated teeth. The latter are used in Elasmobranchii studies to identify taxa and to reconstruct evolutionary trajectories (REF). However, there are problems about taxonomic identification based on qualitative dental characters only. PURDY (2006) pointed out that subjectivity in identification and teeth ontogeny may lead to an incorrect identification. Furthermore, several lineages present similar morphological traits.

Since the Neoselachii are a long-lived group and have faced at least the last three major extinctions, in the present study we analysed whether these large mass extinctions affected the diversification rates of the Neoselachii at their most inclusive level (class) and of their orders separately, at a less inclusive level.

METHODS

Fossil and Current Data

Through the Paleobiology Database (paleobiodb.org, accessed April 11, 2017), we obtained a record of 7,245 fossil occurrences for Neoselachii. The data recovered cover about 358 Mya (Carboniferous period) until the current geological period. We have only included the occurrences identified at the genera level, without specific attribution. Records were checked for synonyms, duplicates, and misspellings, and checked through

the Fossilworks (fossilworks.org) portal and specific literature. Those fossils with uncertain or incomplete taxonomic classification were removed. After applying these criteria, a total of 6,695 occurrences were obtained, belonging to fifteen distinct orders (Table S1). The records of current Neoselachii species were obtained through the work of Weigmann (2016), resulting in 630 species of rays and 509 species of sharks (Table S1). We excluded the order Echinorhiniformes due to small dataset.

Data Analyses

The occurrence data were analysed using PyRate software (http://sourceforge.net/projects/pyrate/), which provides a Bayesian approach to modelling speciation, extinction and diversification (i.e. diversification = speciation – extinction) processes. PyRate performs macroevolutionary analyses from paleontological data, using the information from large-scale databases (Silvestro *et al*., 2014). Parameters of preservation process, origin and extinction times of each species and lineage speciation and extinction rates and their variation over time are estimated through a Markov Chain Monte Carlo algorithm (MCMC) (Silvestro *et al.*, 2015). PyRate assumes that the occurrence data observed result from the interaction between these parameters (Silvestro *et al.*, 2015). The analysis of diversification was carried out with estimates of speciation and extinction times of all species (Silvestro *et al.*, 2015). We ran the PyRate for 500 million generations using 10 replicates. A 20% burn-in was discarded after data analysis. The convergences of the chains were evaluated in the Tracer 1.7 software (Rambaut *et al.*, 2018), with an Effective Sample Size (ESS) greater than 200 being used as a parameter. The graphs of speciation, extinction and diversification rates were generated using the R-3.4.3 platform (Silvestro *et al.*, 2014).

RESULTS

Our results showed that there were no changes in Neoselachii speciation, extinction and diversification rates related to the three mass extinction events (251 Mya, 200 Mya and 66 Mya). Neoselachii showed a constant decline in its speciation rate over time, from the Carboniferous period (approximately 300 Mya) to the present day, showing no peak of decline or increase in this rate (Fig. 1A). The extinction rate of the group presented an increase between approximately 10 Mya and 5 Mya, in the limit between the Miocene and Pliocene epochs (Fig. 1B). The Neoselachii diversification rate was negative from the Pliocene to the present day (Fig. 1C), because they presented an extinction rate higher than the speciation rate over the last 5 Mya. Comparing the richness of genus (Fig. 2) with the diversification presented by the clade (Fig. 1C), it is possible to observe three distinct moments of diversification: i) – positive diversification to approximately 50 Mya, where one can observe an increase in the number of genus; ii) – diversification is equal to zero between 50 Mya and 10 Mya approximately, period which corresponds to a decrease in the richness followed by a period without strong alterations in the number of genus, and; iii) – negative diversification range from 10 Mya to the present, which corresponds to a decrease in the number of genus.

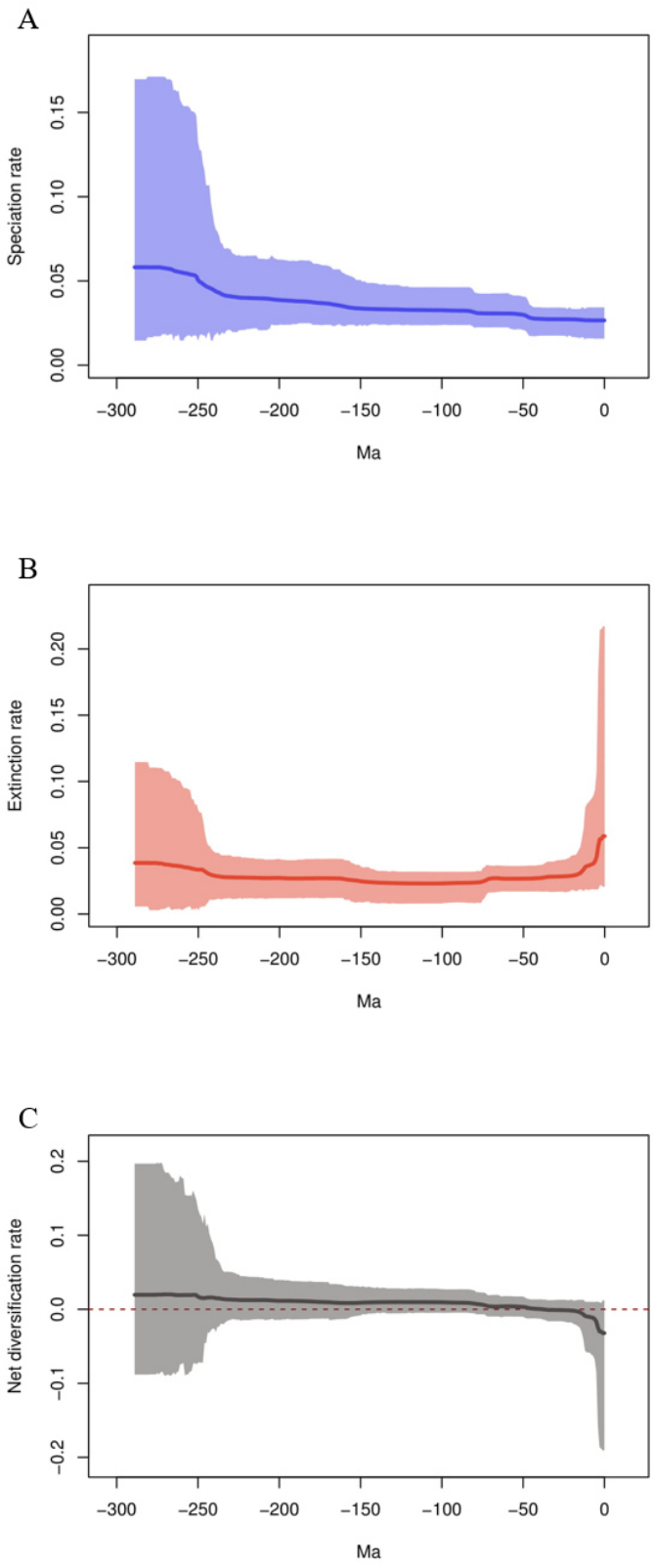

Figure 1. Speciation rate (A), Extinction rate (B) and Diversification rate (C) of Neoselachii. The solid lines represent the average rates and the shaded areas represent 95% Highest Posterior Density (HPD) intervals.

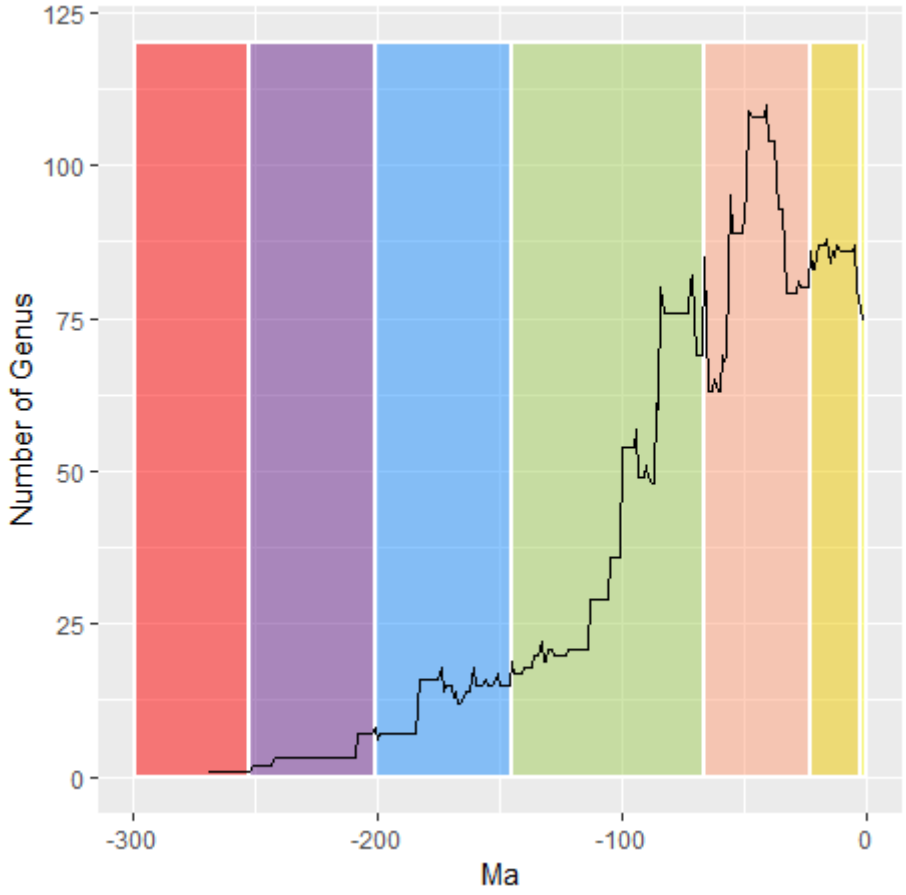

Figure 2. Richness of genus over millions of years. The colours represent different periods: Permian (red); Triassic (violet); Jurassic (blue); Cretaceous (green); Paleogene (pink); Neogene (gold) and Quaternary (yellow).

When analysing the orders separately, our results showed that none of the orders presented changes in diversification rates related to mass extinction events. There was a decline in speciation rates and an increase in extinction rates of Carcharhiniformes, Hexanchiformes, Lamniformes, Myliobatiformes, Pristiformes and Squaliformes around 10 Mya (Fig. 3A - Fig. 3F, Fig. S1-S4). This led to a decline in diversification rates for each of these groups. A different pattern was observed for Rhinobatiformes, which showed a decline in speciation rate and an increase in extinction rate 30 Mya ago (Fig. 3G), resulting in a decline in their diversification rate. The orders Heterodontiformes, Pristiophoriformes, Rajiformes, Rhiniformes, Squatiniformes, Synechodontiformes and

Torpediniformes did not present a relevant variation over time in the analysed rates (Fig. S1-S4). Only for Orectolobiformes was it not possible to obtain the convergences of the Markov chains.

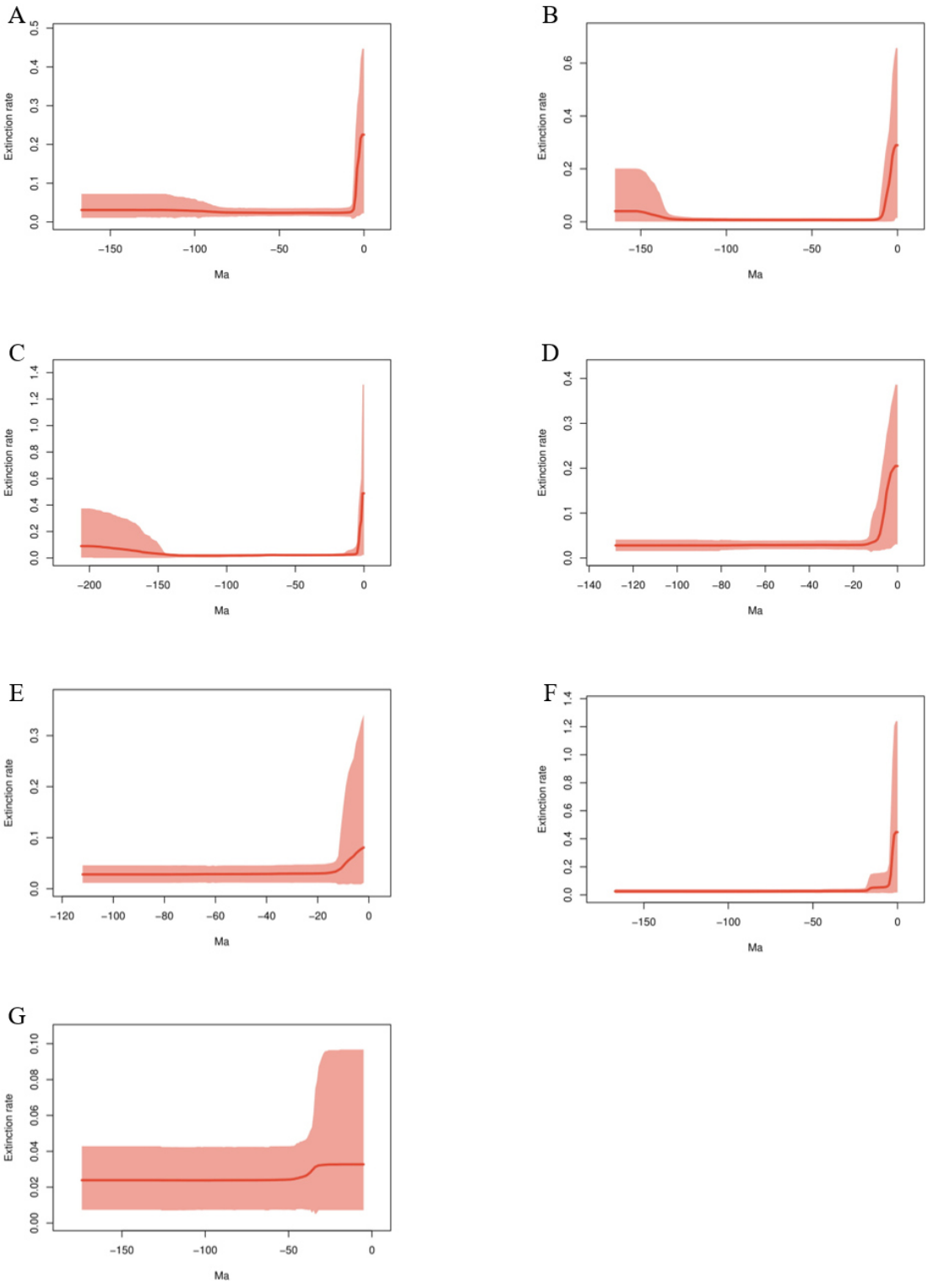

Figure 3. Extinction rates estimated through PyRate software for the orders: Carcharhiniformes (A); Hexanchiformes (B); Lamniformes (C); Myliobatiformes (D); Pristiformes (E); Squaliformes (F); and Rhinobatiformes (G). The solid lines represent the average rates and the shaded areas represent 95% Highest Posterior Density (HPD) intervals.

DISCUSSION

Our results indicate that there were no strong changes in Neoselachii clade diversification rates associated with large mass extinctions. When analysing the orders separately, no changes were also found in diversification rates related to mass extinction events. The main causes of Neoselachii extinctions and speciations, and the characteristics which allowed these animals to survive the great extinctions, have not yet been fully elucidated. On the one hand, eating and living habits may partly explain this evolutionary success. On the other hand, climatic and geological changes, while destroying some niches, have opened new ones (Brose, 2010), allowing the coexistence of species and leading to the adaptive evolution of many others. The survival of a clade to extinction is not random (Jablonski, 2005). Each extinction event has a selectivity, and the wide geographic distribution of the clade is a factor that promotes its survival (Dye *et al*., 1994; Jablonski, 2005; Payne & Clapham, 2012). The cosmopolitan behaviour of Neoselachii may have favoured their survival of great extinctions. Cartilaginous fish appear to be one of the most endangered marine animals today (Dye *et al*., 1994; Myers & Worm, 2005) due to their large body size, low fecundity (Dye *et al*., 1994; Garcia *et al.*, 2008), and habitat in which it lives (Garcia *et al.*, 2008). However, our results show that the last five large mass extinctions have not affected them significantly.

We did not find any evidence of diversification related to mass extinction or immediately after an extinction event in the analysed data. However, this is not consistent with other studies that indicated an increase in diversification rates after mass extinction events. Previous studies have revealed that there have been periods of diversification in the Early and Middle Jurassic (Kriwet & Benton, 2004; Underwood, 2006; Kriwet *et al.*, 2009) and mid to Late Cretaceous periods (Underwood, 2006; Bazzi *et al.*, 2018). Those results are not consistent with the fossil occurrences analysed herein. Kriwet & Benton

(2004) showed that the major extinction of Neoselachii was during the Cretaceous-Tertiary mass extinction; also, in the end of the Paleocene and early Eocene, new families with ecological similarities replaced the extinct families, which recovered the Neoselachian diversity. A possible explanation for this disagreement in the results is that we used more than double the number of species used in previous studies in the current one, incorporating both extinct and extant species. In addition, the analytical approach itself may also be a factor that leads to discrepancies between studies. The PyRate analyses fossil information in a continuous time (not in categories of time intervals) and uses all occurrences of fossils (Silvestro *et al.*, 2014).

The Cenozoic era was marked by three minor extinction episodes between the Eocene-Oligocene (34 Mya) boundaries, at the end of the Miocene (8 Mya) and in the middle of the Pliocene (4 Mya), related to rearrangements in the environment (Janis, 1993). Habitat loss has a direct effect on extinction due to the loss of essential environments required for species to live or complete their life cycle (McDowall, 1992). Rhinobatiformes order presented an elevation in the extinction rate of approximately 30 Mya. After the last mass extinction (66 Mya), the transition between Eocene and Oligocene (E-O) is known as one of the most significant events of history of the Earth (Prothero, 1994). In the E-O transition, the Earth changed from global "greenhouse" to global "ice" house world. Isotopic analyses of oxygen from otoliths of fishes showed that the coldest winters occurred at 30 Mya (Ivany *et al*., 2000). This temperature decrease seems to have driven several marine lineages to extinction (Prothero, 1994; Pearson *et al.*, 2008), mainly those stenothermal animals of tropical regions (Ivany *et al.*, 2000). By observing the geographical distribution of fossils of Rhinobatiformes in the Eocene, it was noted that most are concentrated in tropical regions close to the Mediterranean Sea

(paleobiology.org). Thus, it is possible that a strong cooling of the planet in the E-O transition has been an impetus for the increased extinction rate in Rhinobatiformes.

Between Miocene and Pliocene there were ecological changes, both at the faunistic and floristic levels, caused by an increase in seasonality and a greater aridity of the environment (Janis, 1993). At the end of the Miocene, seas experienced a period of cooling and regression, followed by an abrupt heating and transgression at the beginning of the Pliocene (Haq *et al*., 1987). In the Miocene-Pliocene border (between 10 and 5 Mya), we found an increase in Neoselachii extinction rates and in extinction rates from six of the fifteen analysed orders (Carcharhiniformes, Hexanchiformes, Lamniformes, Myliobatiformes, Pristiformes and Squaliformes), which coincides with large-scale disturbances suffered in the environment at this time. The extinction rates present in the Cenozoic fossil records reveal that all extinctions suffered by the Chondrihchtyes during this era were at the local level (Dulvy *et al.*, 2003). In tropical marine environment, in late Miocene-Pliocene, the main primary producers, red coral algae, suffered their greatest extinction (Aguirre *et al*., 2000). These changes in the faunal composition, with extinction of producers and primary consumers, may have caused a cascade effect in other groups (Harnik *et al.*, 2012), and thus also contributed to a significant increase in the extinction rates of Carcharhiniformes, Hexanchiformes, Lamniformes, Myliobatiformes, Pristiformes Rhinobatiformes and Squaliformes. Additionally, in the last ten million years there has been a rapid taxonomic and ecological radiation of cetaceans, with the emergence and diversification of several lineages (Milinkovitch, 1995). Changes in sea level during the Eocene, Miocene and Pliocene influenced dispersal movements of these mammals (Janis, 1993), which start to occupy the same environments as Neoselachii. This period of cetacean dispersion coincides with the increase in extinction rate observed for the orders Carcharhiniformes, Hexanchiformes, Lamniformes, Myliobatiformes,

Pristiformes and Squaliformes, which may indicate a possible competition between these groups. Species belonging to distinct clades that present ecological similarities can compete and may lead to clade substitution (Valkenburgh, 1999).

Mass extinctions were important events that led to macroevolutionary changes (Jablonski, 2005); however, many marine lineages were extinguished during intervals between large extinctions, characterised by background extinction rates (Alroy, 2008; Peters, 2008). Species that were extinguished in these ranges generally do not directly suffer from great abiotic effects, but are affected by ecological crises and declining communities (Roopnarine, 2006). In this way, the local extinctions compromise biodiversity by altering trophic paths and habitats for other species (Pitcher, 2001). The extinction suffered by Neoselachii during Miocene-Pliocene boundary was at the local/regional level, and was possibly more associated with such ecological crises and biotic interactions than with global climatic events.

Although our results indicate that the Neoselachii lineage has been declining in the last 10 Mya, human pressure is accelerating the extinction process (Hilton-Taylor, 2000; Vié *et al*., 2009). Background extinction rates throughout fossil records show periods of decline and increase (Harnik *et al.*, 2012). However, the planet is currently undergoing a new period of high extinction rate, the Holocene extinctions, the causes of which are anthropogenic (Harnik *et al.*, 2012). These extinctions are equated at the number of losses to large mass extinctions (Wake & Vredenburg, 2008), and are classified by many researchers as the sixth mass extinction (Ceballos *et al.*, 2015; Ceballos, *et al*., 2017). Although the causes of past extinctions are different from current extinctions, its consequences to organisms have similar effects. It is estimated that 80% of current marine extinctions come from a single source of threat, where the largest threats, according to World Conservation Union categories, are predatory hunting (55%) and habitat

loss/degradation (35%) (Hilton-Taylor, 2000). In addition to these threats, marine species currently face pollution, ocean acidification, anoxia, global warming (Dulvy *et al.*, 2003; Payne & Clapham, 2012), diseases and invasive species (Dulvy *et al.*, 2003).

The current extinctions of Chondrihcthyes have been associated with exploitation (predatory hunting) at the local/regional level (Dulvy *et al.*, 2003). Sharks have a slow growth rate, mature late, have few offspring, and have low population growth, making them vulnerable to population loss, with low restructuring capacity in predatory hunting (Vié *et al.*, 2009). Impacts caused by anthropogenic actions in the marine environment will increase in the coming years, causing an interaction between various threats (Vié *et al.*, 2009; Burrows *et al.*, 2011). How these threats will interact and how this will affect marine species remains uncertain (Harnik *et al.*, 2012). However, studies show that the effects of combining two or more threats are present in both past and present extinctions (Clapham & Payne, 2011). Understanding how these interactions have affected species in the past helps to study future risks through projections of climate change and environmental impacts (Harnik *et al.*, 2012). According to our analysis, climatic changes related to large mass extinctions, such as glaciers advance and continental rearrangement did not affect the diversification of Neoselachii. Events of small-scale extinctions in the Paleogene and Neogene period, related to the cooling of the planet and dispersion of possible competitors, may be associated with the extinction rates of sharks and rays. However, current factors that indicate a possible sixth extinction are different, and the life history characteristics of Neoselachii make them especially vulnerable at this time.

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SUPPLEMENTARY MATERIAL

Table S1: Neoselachii Dataset

	Extinct Species/Genus	Fossil occurrences	Extant Species
Sharks Orders			
Carcharhiniformes	86	1306	284
Echinorhiniformes	—	—	2
Heterodontiformes	19	101	9
Hexanchiformes	25	187	6
Lamniformes	162	2654	16
Orectolobiformes	72	379	45
Pristiophoriformes	3	33	8
Squaliformes	42	195	119
Squatiniformes	11	128	20
Synechodontiformes	43	326	—
Ray Orders			
Myliobatiformes	112	855	210
Pristiformes	26	172	5
Rajiformes	39	161	285
Rhiniformes	10	47	8
Rhinobatiformes	31	128	53
Torpediniformes	8	23	69

Figure S1. Speciation and Diversification rates of Carcharhiniformes (A, B); Hexanchiformes (C, D); Lamniformes (E, F); and Myliobatiformes (G, H).

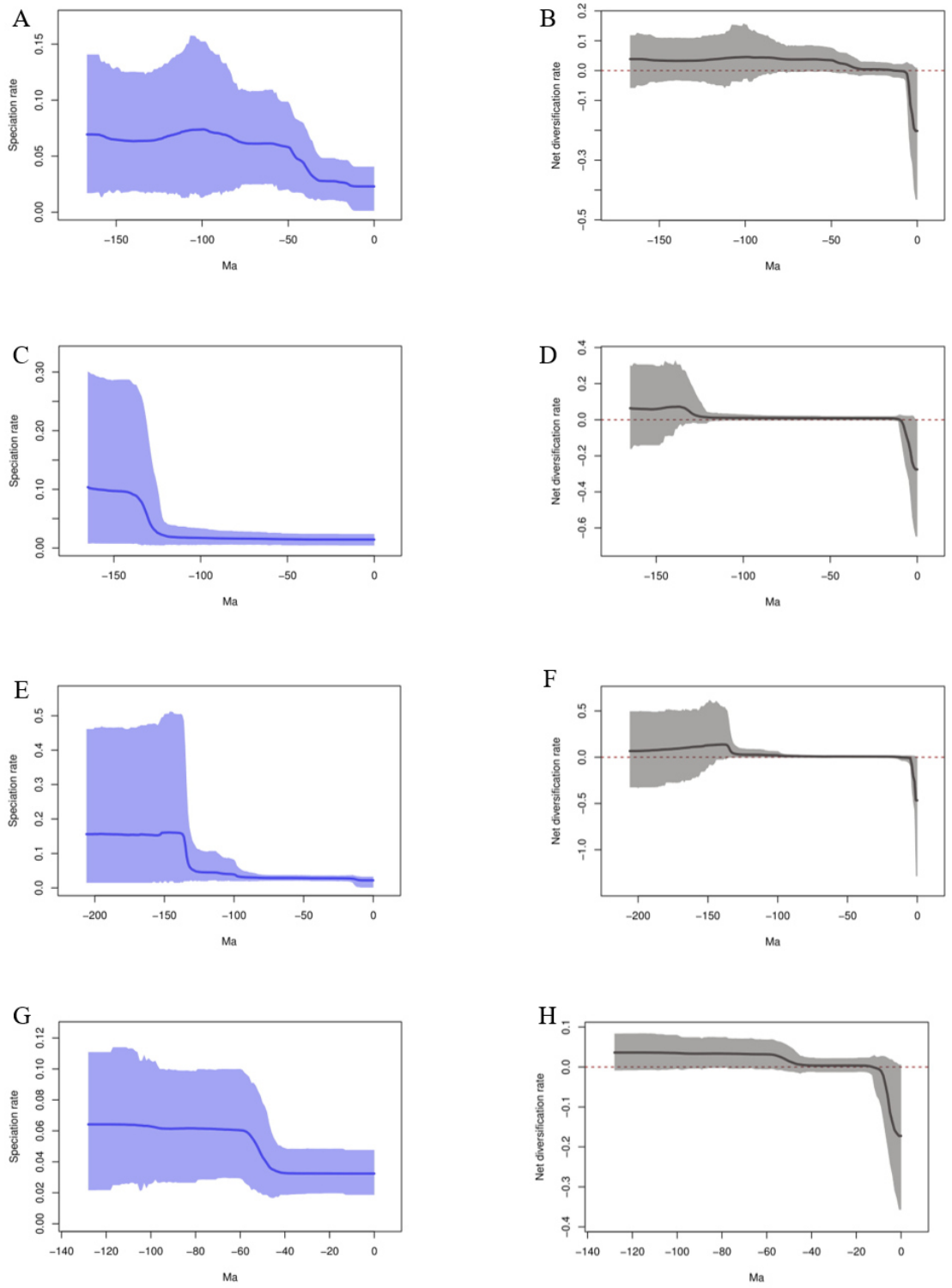


Figure S2. Speciation and Diversification rates of Pristiformes (A, B); Squaliformes (C, D); and Rhinobatiformes (E, F).

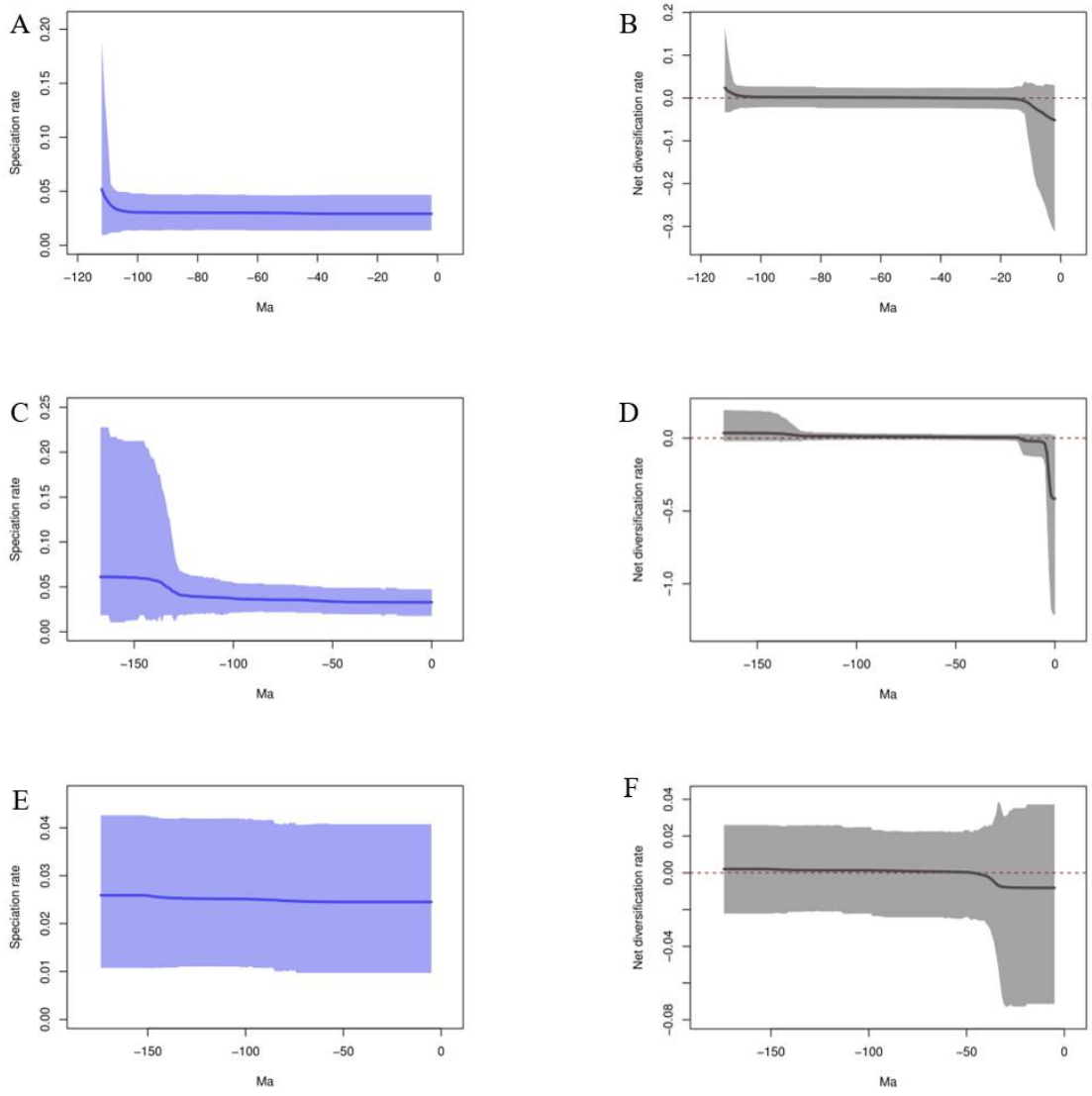


Figure S3. Speciation, Extinction and Diversification Rates of Heterodontiformes (A, B, C); Pristiophoriformes (D, E, F); Rajiformes (G, H, I); and Rhiniformes (J, K, L).

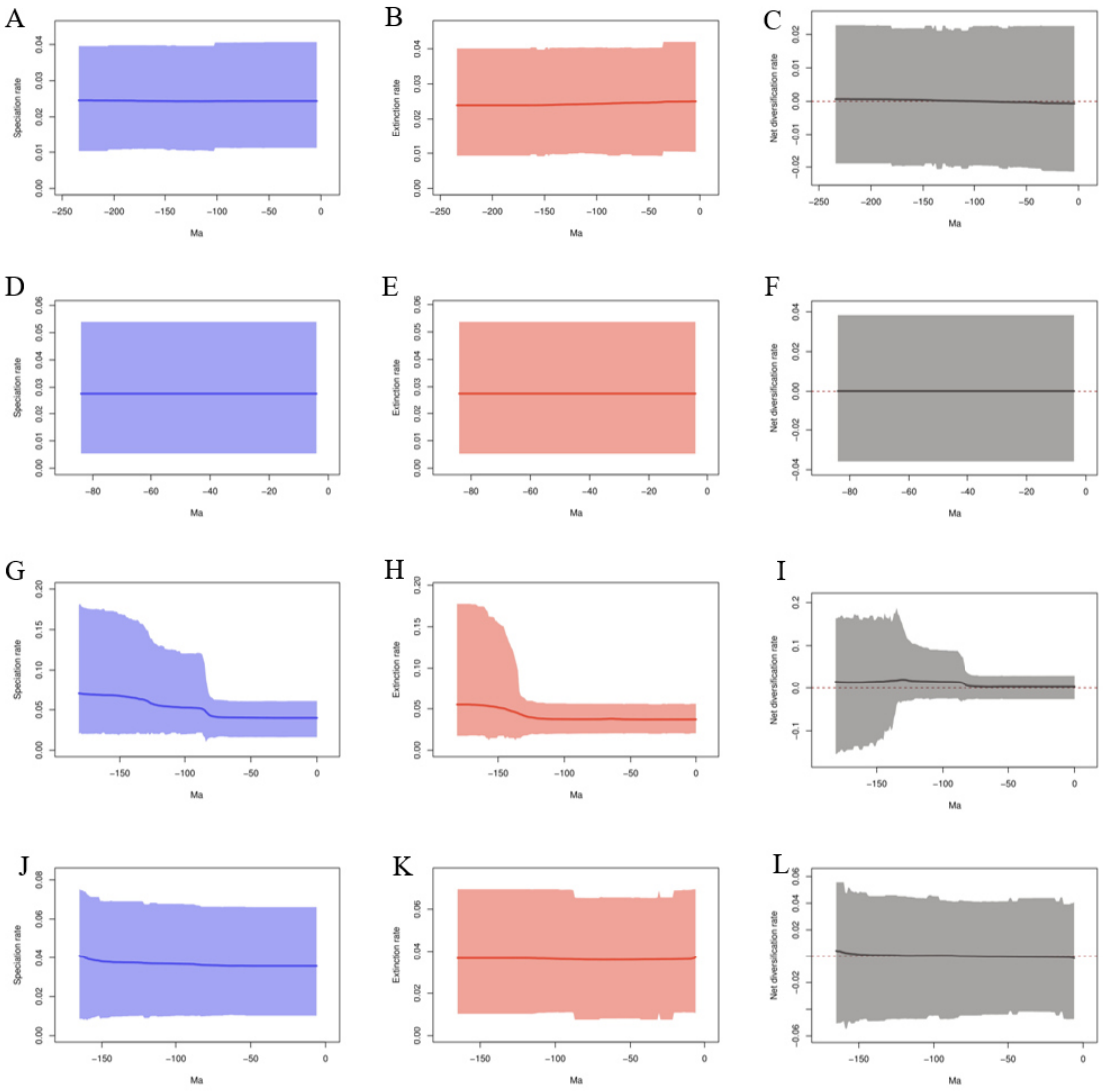
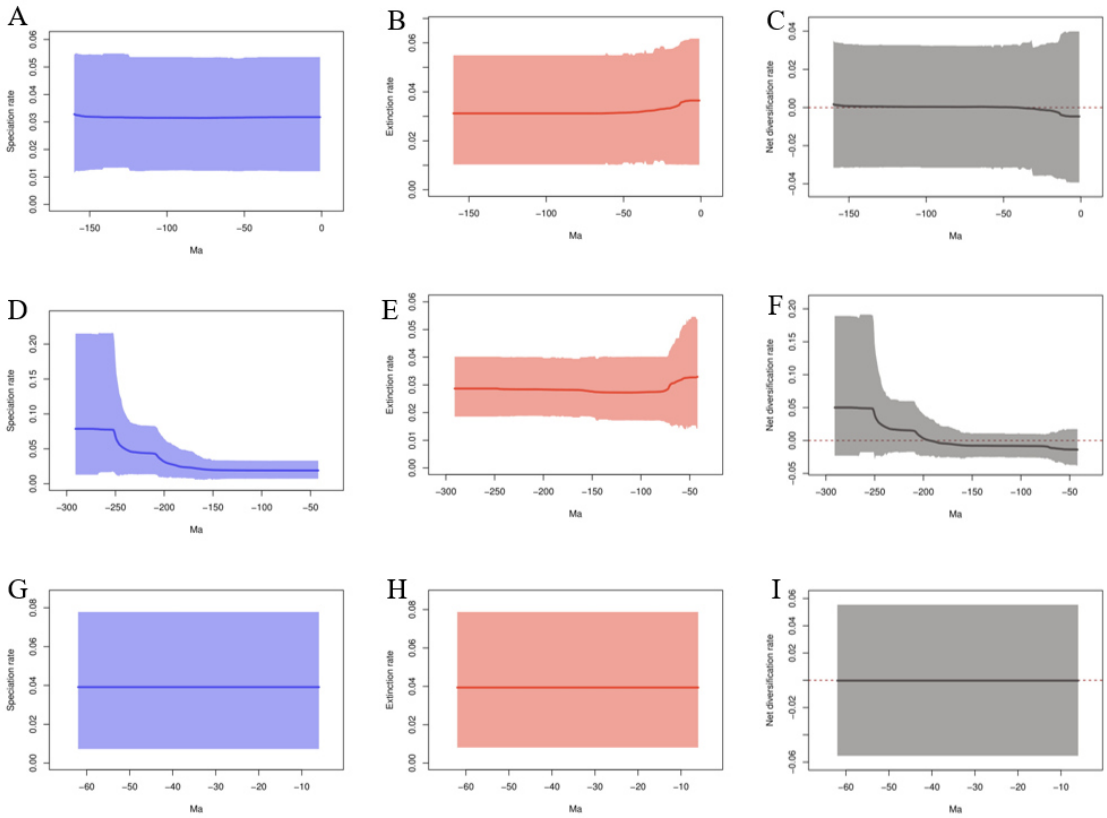


Figure S4. Speciation, Extinction and Diversification Rates of Squatiniformes (A, B, C); Synechodontiformes (D, E, F); and Torpediniformes (G, H, I).



If 'competition' exists at supraspecific levels, a new theory of competition in macroevolution will have to be developed.

— Benton, 1987 (331)

CHAPTER II - Environmental Changes and Competition increase the extinction rate of Neoselachii in the late Cenozoic

ABSTRACT

Speciation and extinction events model biodiversity through a replacement of species, driven by biotics and abiotics factors, including ecological interactions. Most studies of macroevolutionary patterns are about terrestrial lineages, and works of marine biota is still rare. Previous work found an increase in extinction rates of Neoselachii on Cenozoic Era. Some important contributory phenomenon are environmental changes and intraclade and interclade competition. In this chapter we analysed the role of temperature, sea level and intraclade competition among Neoselachii orders and interclade competition between Neoselachii orders and Delphinidae (Mammals: Odontoceti) in the extinction rates of Neoselachii orders. We found that the decrease in temperature contributed to decline in extinction rates of all orders here analysed. Alterations in sea level affected four of seven orders here studied. Finally, our results showed intraorder competition among six orders, where Lamniformes extinction rates were affect by Pristiformes, Rajiformes and Rhinobatiformes diversification, and the extinction rate of Squaliformes declined as a result of competition with Orectolobiformes. Interclade competition revealed that Delphinidae diversification caused an increase in extinction rates of Hexanchiformes, Myliobatiformes and Squaliformes. Thus, multiple factors seem to have affected the increase in extinction rates of Neoselachii orders in the last 30 Mya.

Key words: Delphinidae, elasmobranchs, interaction, PyRate, sea level, temperature

INTRODUCTION

Speciation and extinction events modulate the biodiversity. Extinction is omnipresent in the history of biodiversity. As new species arise and increase in diversity, most of them decrease and get replaced (Silvestro *et al.*, 2015). These changes in biodiversity are driven by abiotics and biotics factors, including climate changes and ecological interactions. Geological changes on Earth's surface are pointed as the major causes of extinction events. Eustatic sea level changes (Smith *et al.*, 2001) and decrease in water temperature (Clarke, 1993) have been associated with extinction on marine environments. Smith (2001) describe three potential mechanisms used to explain why sea level can lead to an extinction event: (i) changes in sea level can change ecologically critical zones surface area over the continental shelves; (ii)expansion of the oxygen minimum zone onto continental shelf, triggered by enhanced surface-water productivity as terrestrial-derived nutrients are brought into the system and (iii) increase in the sea level can modify oceanographic circulation pattern. Temperature have direct effect on water properties, for example viscosity, gas and carbonate solubility, thus, alterations on temperature will change others environmental factors relevant to marine animals (Clarke, 1993). It is also known that ectotherms and endotherms animals are temperature strictly dependent (Jameson, 1981; Pimiento *et al.*, 2019), and any alteration on temperature will affect their thermoregulation strategies.

Although the diversification of a lineage is commonly linked to abiotics features, such as climate changes, biotic interactions could also influence dynamics of speciation and extinction, particularly competition (Benton, 2009; Valkenburgh, 2007). Usually, competition is seen among closely related species; however, it may also occur among species phylogenetically distant with similar ecology (Valkenburgh, 1999). At a macroevolutionary view, there are two ways to competition takes place, passive

replacement, when one clade inhibits a competing clade to radiate or active displacement, when the increase in a clade diversity provokes the decrease of another clade by outcompeting it on limited resources (Sepkoski, 1996; Silvestro *et al.*, 2015). Although the competition concept is also used in palaeontology, it is hard to demonstrate how one species can aid the extinction of another (Birch, 1957). Among the effects of interclade competition, two can be used in the study of extinction: the number of coexisting species, where competition may reduce the number of species coexisting in an area, and the number of species per genus (Benton, 1987). In competitive interactions, increase in species diversity supress speciation rates and/or increase extinction rates (Silvestro *et al.*, 2015).

Pimiento *et al*. (2017) found out high extinction rates of marine megafauna during the Pliocene (5 Mya). When analysed each clade individually, they found that all marine groups, with exception of sea birds, presented elevated extinction rates in the Paleocene. Since the marine megafauna play major roles in ecosystem (Malhi *et al.*, 2016) studies about the extent and consequences of marine megafauna extinctions are primordial (Pimiento *et al.*, 2017). Neoselachii, clade which comprising sharks and rays, originated approximately 358 Mya (Carboniferous period) (Duffin e Ward, 1983; Gunnell, 1933) and experimented his greatest diversity in the oceans in the Jurassic-Cretaceous period (201 Mya-66 Mya) (Benton, 2005; Underwood, 2006). Previous work (chapter I) pointed out that there was no alteration in the diversification rates of Neoselachii until 30 Mya It was found a pattern of increasing extinction rate in recent evolutionary dynamics of six orders (Carcharhiniformes, Hexanchiformes, Lamniformes, Myliobatiformes, Pristiformes and Squaliformes) in the last 10 Mya, which coincides with the cetaceans radiation (Milinkovitch, 1995). Although phylogenetically distant, Neoselachii and Delphinidae (Cetacea) present ecological and morphological similarities, since both are

macropredators and occupied the same habitat (Andreu *et al.*, 2018) and present a fusiform body shape (Donley *et al.*, 2004). During this period the world also experienced periods of cooling (Haq, Hardenbol e Vail, 1987) and changes in sea level (Cione *et al.*, 2007). Once sharks and rays are mostly ectothermic animals (Pimiento *et al.*, 2019), is expected that planet's cooling events can have negative effects on the Neoselachii. On the other hand, since sharks are mostly fusiform shaped-body and rays are more flattened (Wilga e Lauder, 2004), decrease in sea level will favour flattened animals, once they are found in shallow waters (Andreu *et al.*, 2018).

In this work we investigated whether temperature, sea level and competition within (Neoselachii) and among clades (Delphinidae) affected extinction rates of Neoselachii orders throughout its evolutionary history.

METHODS

Fossil and Extant Data

Fossil occurrences were extracted from the Paleobiology Database (paleobiodb.org, accessed April 2017), which only records at the genus or species level were included. Data were checked through the Fossilworks (fossilworks.org) and specific literature for synonymy, duplicates and grammatical errors, and records with erroneous or uncertain taxonomic classification were excluded from the analysis, resulting in 6,695 occurrences distributed among fifteen orders covering 358 Mya (Carboniferous period) until the current period. The list of current species was obtained through the work of Weigmann (2016), counting 630 species of rays and 509 species of sharks, separated in fifteen orders. We excluded the order Echinorhiniformes from analyses because it presents only current species.

Fossil Data Analysis

We use a Bayesian approach to model extinction, implemented within the program PyRate (http://sourceforge.net/projects/pyrate/). This approach uses paleontological data obtained from large-scale databases to perform macroevolutionary analyses (Silvestro, Salamin e Schnitzler, 2014) and assumes that the observed data are results of the interactions between the preservation processes, the time of origin and extinction of each species and the speciation and extinction rates of each lineage and their variation over time (Silvestro *et al.*, 2015). These parameters were estimated by the Monte Carlo Markov Chain Method (MCMC) (Silvestro *et al.*, 2015). For the analyses of diversification, the speciation and extinction times of all species were estimated (Silvestro *et al.*, 2015). We ran the PyRate for 500 million generation with 10 replicas and a 20% burn-in phase. Through the software Tracer 1.7 (Rambaut *et al.*, 2018) we analysed the chains convergence using an Effective Sample Size (ESS) greater than 200 as a parameter.

Temperature-Dependent and Sea Level-Dependent Diversification Analysis

To test the correlation between abiotic factors (temperature and sea level) and the extinction rates of Neoselachii, we used a birth-death model with variable rates in time (Silvestro *et al.*, 2015). The correlation between changes in birth–death rates and temperature and sea level changes is quantified by the parameter $\gamma\mu$, where $\gamma > 0$ indicates positive correlation and $\gamma < 0$ indicates negative correlation (For more details, see Silvestro *et al.*, 2015). For the analysis at the level of order, we selected only those orders that presented variation in the extinction rate in Cenozoic Era, resulting from the analysis of the fossil data described above performed in chapter I of this work (Carcharhiniformes, Hexanchiformes, Lamniformes, Myliobatiformes, Pristiformes, Rhinobatiformes and Squaliformes). Temperature and sea level data were extracted from Zachos *et al*. (2008)

and Miller *et al*. (2005) through rPANDA package – Phylogenetic ANalyses of DiversificAtion (https://github.com/hmorlon/PANDA/tree/master/data). All graphics of this work were generated using R-3.4.3 plataform.

Competition Among Clade

For competition analysis we also select only those orders that showed alteration in the extinction rate described in chapter I. To test the competition among clades, we compiled the Delphinidae data from the Paleobiology Database (112 extinct and 37 extant species). We used a birth-death model developed by Silvestro *et al*. (2015), called Multiple Clade Diversity Dependence, which evaluates the effect of competition between and within the clades in their diversity, and uses Bayesian variables to together analyse all clades and estimate for each clade the extinction rate, the marginal competition probability and competition parameters which quantify the diversity dependence intensity between each pair of clades. The parameter g quantifies the diversity intensity dependence among clades, which $g > 0$ indicates competition and $g < 0$ indicates positive interaction. We ran Pyrate for 150 million generation and 150 replicates. The chains convergence was evaluated through Tracer 1.7 (Rambaut *et al.*, 2018) using an Effective Sample Size (ESS) greater than 100[1] as a parameter. (For more details, see Silvestro *et al.*, 2015.)

RESULTS AND DISCUSSION

The fossil data analysis carried out on chapter one showed that the whole clade and only seven orders, Carcharhiniformes, Hexanchiformes, Lamniformes, Myliobatiformes, Pristiformes, Rhinobatiformes and Squaliformes, presented an increase in the extinction rate in the Cenozoic Era. Our results suggest that temperature variation

[1] The analyses will be redone with a larger number of generations. We believe that the results will not change much; however, it is expected to use an ESS > 200.

is strongly negatively correlated with extinction rates of Neoselachii clade (Fig. 1A) and Carcharhiniformes, Hexanchiformes and Lamniformes (Fig. 1B–D), and lightly negatively correlated with Myliobatiformes, Pristiformes, Rhinobatiformes and Squaliformes (Fig. 1E–H), which means that changes in temperature increase the extinction rates of them. The orders here analysed present as thermoregulatory strategy the ectothermy, except for Lamniformes that are mesothermic (Pimiento *et al.*, 2019). As these animals depend on environment temperature to control the body temperature (Jameson, 1981), ectotherms present difficulty to thermoregulate (Lutterschmidt, Lutterschmidt e Hutchison, 2003). Low temperatures lead to a slower growth and a larger body size in ectotherms, retarding reproduction compared to organisms in warm environment and decreasing the chances of individuals in cold areas survive to reproduce (Angillietta, Steury e Sears, 2004). Due to the decrease in global temperatures in Oligocene (30 Mya) and in late Miocene to Pliocene (10 Mya – present) (Fig. 2), Neoselachii were not able to thermoregulate or reproduce, which reflected in the decrease in their extinction rates. Study with marine megafauna suggested that thermoregulation was the main attribute responsible by extinction of ectotherms and mesotherms in Pliocene (Pimiento *et al.*, 2017). We found that animals more fusiform were more affected by the decrease in temperature than flattened animals. From the point of view of heat conservation this is contradictory, since fusiform animals retain heat better than flattened (Tilkens *et al.*, 2007). However, it has been observed that fusiform animals require warm waters due to higher availability of dissolved oxygen in these environments, which facilitates their locomotion and the capture of prey (Andreu *et al.*, 2018). So, a decline in dissolved oxygen leads to a low swimming performance (Penghan, Cao e Fu, 2014). In contrast, flattened ones are not as dependent on hot water given they present different types of locomotion and capture of prey (Andreu *et al.*, 2018). Our results are

consistent with previous study which suggested that the extinction of fishes from cold oceans can be explained by the decline in temperature during the Cenozoic (Cione, 2002).

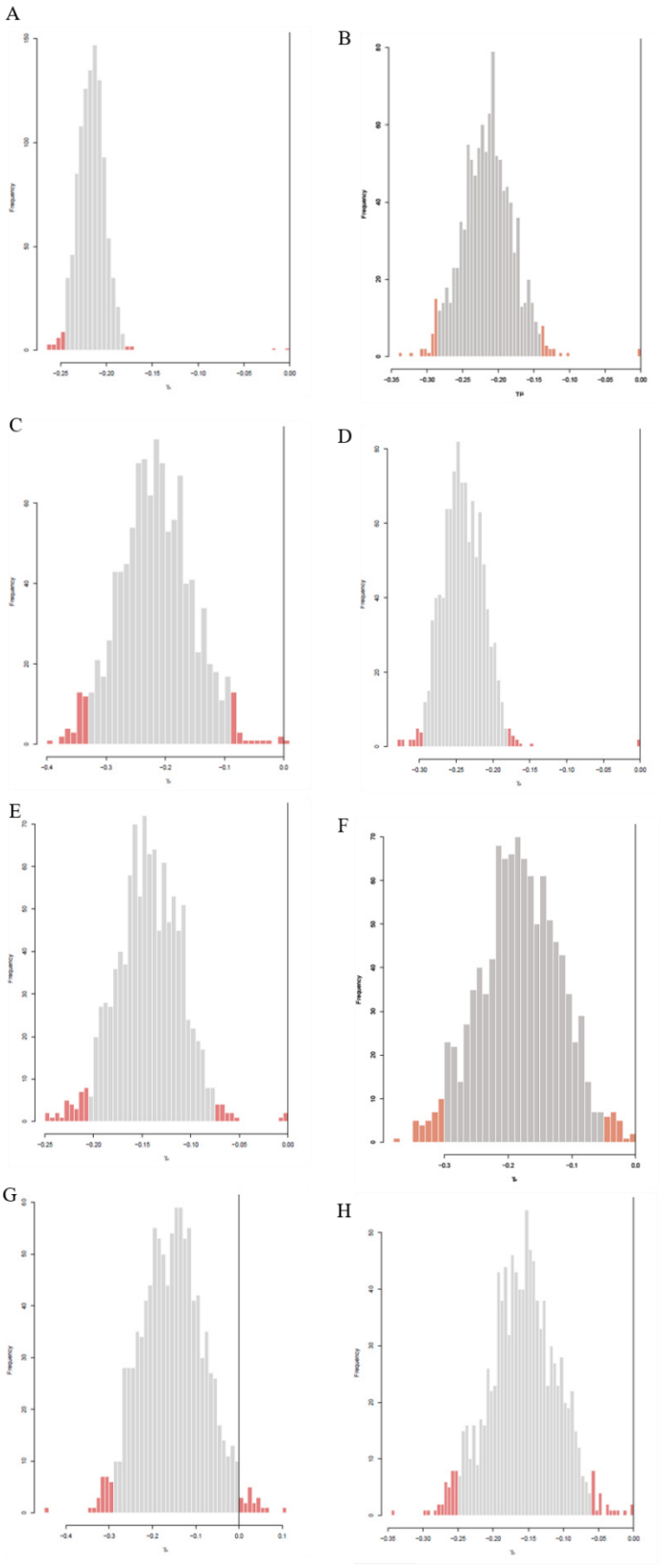


Figure 1. Temperature correlation with extinction rates: Neoselachii (A), Carcharhiniformes (B); Hexanchiformes (C); Lamniformes (D); Myliobatiformes (E); Pristiformes (F); Squaliformes (G); and Rhinobatiformes (H). Grey areas represent 95% credible intervals (95% CIs).

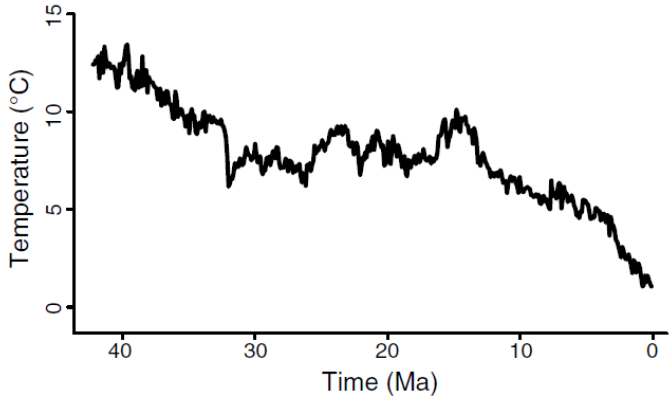


Figure 2. Relative Global Temperature (extracted from Silvestro et al., 2015).

We found that changes in the sea level correlate negatively with extinction rates of Neoselachii (Fig. 3A) and Carcharhiniformes, Hexanchiformes, Lamniformes, and Myliobatiformes (Fig. 3B-E). Pristiformes, Squaliformes and Rhinobatiformes extinction rates did not show significative correlation with sea level alterations (Fig. S1). Decrease in sea level occasioned reduction of habitat (Pimiento *et al.*, 2017; Smith *et al.*, 2001), mainly on continental shelves (Smith *et al.*, 2001). These changes in the available area provoking significant population stress (Smith *et al.*, 2001). Also, habitat loss increases the number of coexisting species, and may increase competition. Appropriated habitats were destroyed during Miocene-Pliocene due to decrease in sea level, leading to local extinction of sharks' species after reaching its extinction point (Cione *et al.*, 2007). Shallower seas favour flattened animals, since they are often found on continental shelves and shallow areas (Andreu *et al.*, 2018). The orders that were most affected by sea level alterations present a fusiform body shape, being more commonly found in deep waters (Andreu *et al.*, 2018). Eustatic inflexions are associated with the expansion of the minimum zone of oxygen over intercontinental seas, generated by an increase in the productivity of surface-water while nutrients from continent are inserted into the system (Hallam e Wignall, 1999; Smith *et al.*, 2001). These anoxic conditions were pointed out

as the main cause of mass extinction (Hallam e Wignall, 1999), therefore, alterations on sea level during Cenozoic may have contributed to the observed extinctions of Neoselachii for the period.

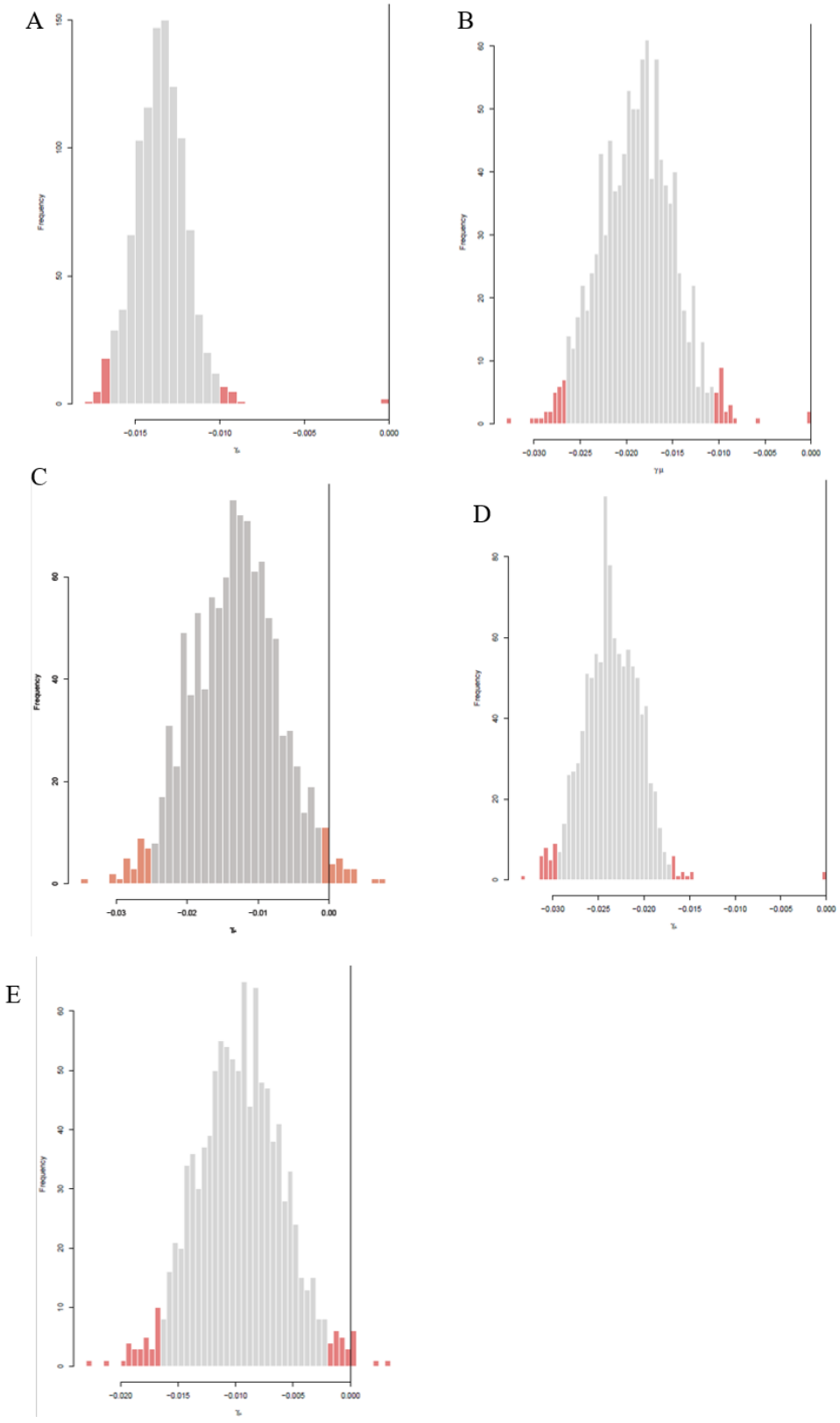


Figure 3. Sea Level correlation with extinction rates: Neoselachii (A), Carcharhiniformes (B); Hexanchiformes (C); Lamniformes (D); Myliobatiformes (E). Grey areas represent 95% credible intervals (95% CIs).

In relation to competition analysis, we find that competition played a considerable role in Neoselachii orders extinction rates (Fig. 4). All seven orders were affected by the diversification of others orders of Neoselachii and/or phylogenetically distant competitors. The increase on extinction rate observed in Lamniformes is attributed to a balance between competition with Rajiformes and Rhinobatiformes diversifications and a positive effect of Pristiformes diversifications. It was also observed a unidirectional interaction between Orectolobiformes and Squaliformes. Although it is difficult to show how one group influence in the extinction of other group, occasionally evidence is enough to give some idea about what could have happened (Birch, 1957). These competitive interaction among Neoselachii orders can be associated with ecological similarities and niche overlap (paleobiodb.org) between these groups. The body shape can be associated with prey capture strategies and occupation of similar habitats (Andreu *et al.*, 2018). Furthermore, Orectolobiformes and Squaliformes are closely related (Andreu *et al.*, 2018). There is evidence that Lamniformes would be competitively superior because they are mesothermic (Pimiento *et al.*, 2019); however, due to large body size in in comparison with the others, they present a greater demand for oxygen (Andreu *et al.*, 2018). As a result, the decline in temperature made them competitively inferior compared to the other groups. Competition with Delphinidae provokes an increase in extinction rates of Hexanchiformes, Myliobatiformes and Squaliformes (Fig. 4). In the Early Pliocene, cetaceans experimented a rapid taxonomic and ecological radiation (Milinkovitch, 1995), followed by dispersal events (Janis, 1993). Thus, Delphinidae and Neoselachii start to coexist. The influence of Delphinidae diversification into Neoselachii orders extinction is problaby due to: (i) similar ecology (Andreu *et al.*, 2018), since Hexanchiformes, Myliobatiformes, Squaliformes and Delphinidae are considered macropredators (Andreu *et al.*, 2018); (ii) similar morphology, both with fusiform body shape (Donley *et al.*,

2004); and (iii) they had lived in the same enviroment (paleobiodb.org; Andreu *et al.*, 2018). Because they are endothermic animals (Torres-Romero, Morales-Castilla e Olalla-Tárraga, 2016), Delphinidae becomes competitively superior in this period of colder temperatures. Additionally, Delphinidae diversification had increased its own extinction rate (Fig. 4).

Although we found out that intraclade and interclade competition occurs among Neoselachii lineage, our results are not in accordance with previous analysis (Myers e Lieberman, 2011) that did not find significant evidence for competitive replacement between sharks. Benton (1996) in his work suggested that competitive replacement played a small role on tetrapod evolution, especially in the last 10 Mya. However, there are several examples from fossil record on literature of groups which lived in the same place for a time with similar adaptive type, as one increased the other decreased to extinction (Darwin, 1859; Simpson, 1950). Simpson (1950) argue that, in these cases, possibly the competition drove on group to extinction, even though this may not be true.

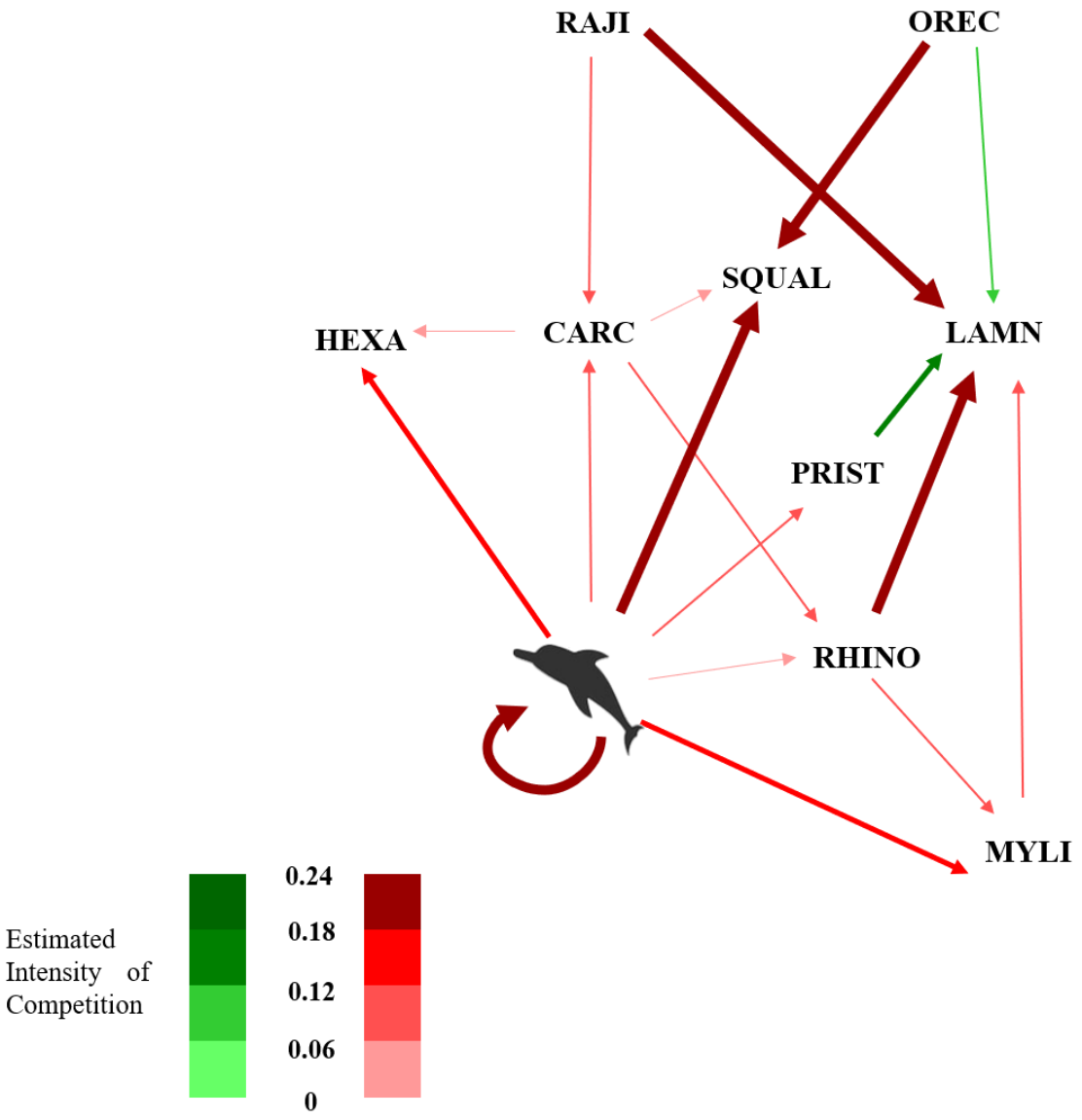


Figure 4. Network showing the competitive effect imposed by each individual clade/order on the other clades'/orders' extinction rate. Arrows shape indicates the direction and intensity of competition. Red arrows indicate the competition and green arrow indicate positive interactions. CARC = Carcharhiniformes, HEXA = Hexanchiformes, LAMN = Lamniformes, MYLI = Myliobatiformes, OREC = Orectolobiformes, PRIST = Pristiformes, RAJI = Rajiformes, RHINO = Rhinobatiformes and SQUAL = Squaliformes.

Macroevolutionary patterns studies are still scarce for marine clades. Lineages diversification is dependent of environmental factors and ecological interactions. Our study strongly support that decrease in temperature, sea level alterations and competition among orders and interclade played an important role in Neoselachii orders diversification. Previous works pointed out the consequences of decline in temperature in sharks' extinction, due to thermoregulation strategy and body shape of this group, which was consistent with our results. Alterations on sea level, found in our analyses as a driver of the decrease in extinction rates in four Neoselachii orders, also was related as a cause of marine extinctions, resulting in population stress, reduction of habitat, anoxic conditions and extinction over food chain by famine, leading to a cascade effect. Our results suggest that competition among sharks' orders did not show strong influence on Neoselachii orders extinction rates, except by the unidirectional interactions between Orectolobiformes and Squaliformes; however, rays orders and Delphinidae diversifications had a strong effect on Neoselachii orders extinction rates. This suggested that similar ecology and coexistence at the same time exercise more influence on competition than morphological similarities. Our results point to multiple factors acting to increase the extinction of Neoselachii in the last million years. These factors were here analysed separately; however, one cannot rule out there are synergistic effects among them.

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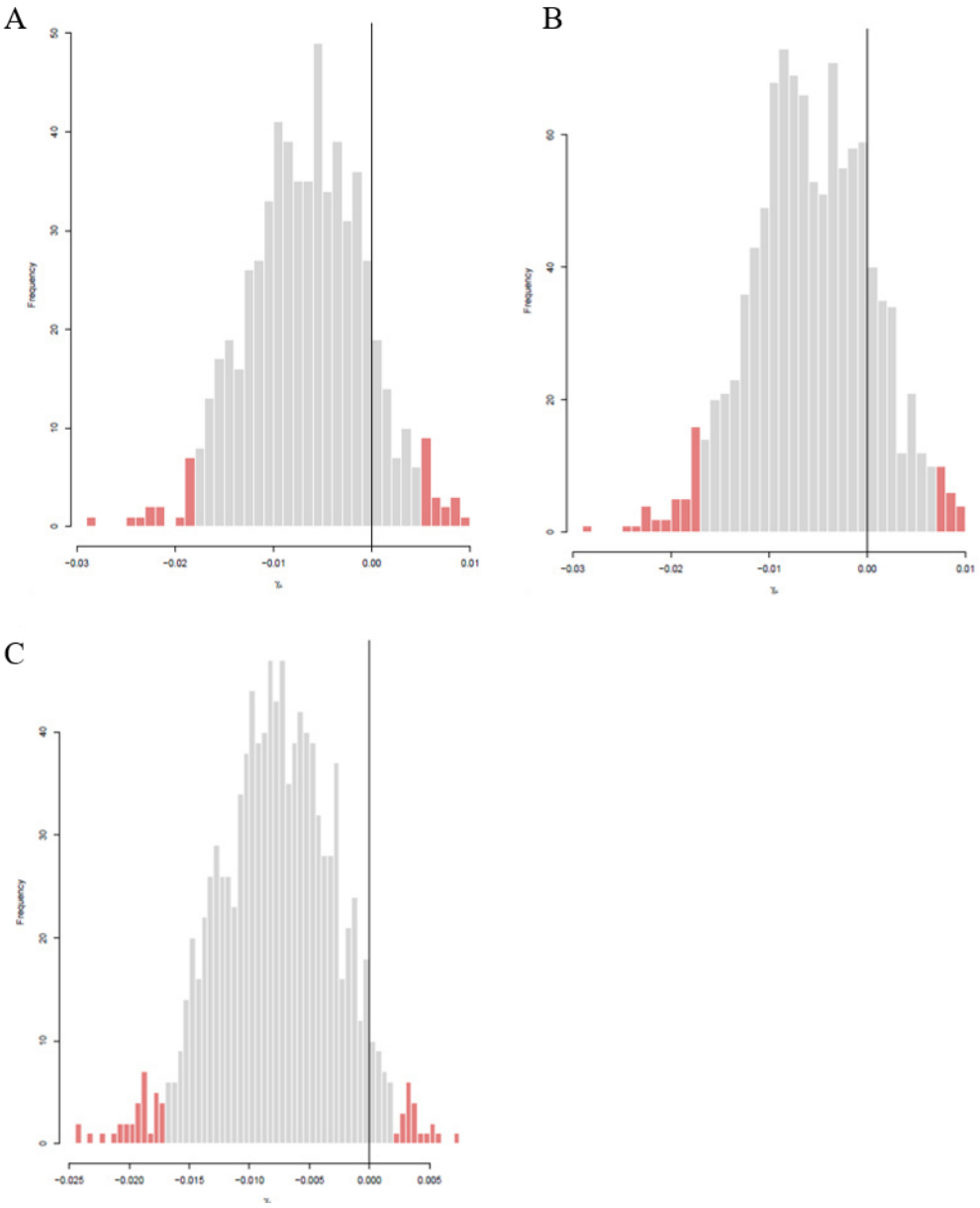
SUPPLEMENTARY MATERIAL

Figure S1. Temperature correlation with extinction rates of: Pristiformes (A), Rhinobatiformes (B) and Squaliformes (C). Grey areas represent 95% credible intervals (95% CIs).



CONCLUSÃO GERAL

Os resultados apresentados na dissertação mostraram que, embora os Neoselachii tenham enfrentado as três últimas grandes extinções sem terem sido diretamente afetados, fatores ambientais e ecológicos contribuíram para um aumento significativo nas taxas de extinção das ordens do grupo, e do grupo como um todo. Os principais pontos a serem destacados são:

- Não houve alterações nas taxas de diversificação dos Neoselachii, a nível de clado ou ordem, relacionadas às Grandes Extinções em Massa;
- Sete das quinze ordens analisadas apresentaram um aumento nas taxas de extinção no final da Era Cenozoica. Para os Rhinobatiformes esse aumento se deu há 30 Ma, e para os Carcharhiniformes, Hexanchiformes, Lamniformes, Myliobatiformes, Pristiformes and Squaliformes esse aumento foi por volta de 10 Ma;
- A diminuição da temperatura global no Oligoceno (30 Ma) e no Mioceno-Plioceno (10 Ma – presente) afetaram todas as sete ordens de Neoselachii que são, em sua maioria, animais ectotérmicos, dificultando a termorregulação dos mesmos, refletindo na sua reprodução e sobrevivência;
- O decréscimo na temperatura também afetou negativamente as ordens estudadas uma vez que a maioria dos tubarões possui corpo em formato fusiforme, já que as formas maiores e mais arredondadas necessitam de uma maior disponibilidade de oxigênio dissolvido em água e a diminuição de temperatura levou a uma diminuição da disponibilidade de oxigênio;
- Diminuição no nível do mar afetou significativamente Carcharhiniformes, Hexanchiformes, Lamniformes, and Myliobatiformes devido à redução e destruição de habitats e condições anóxicas;
- A competição intraclado foi mais forte entre Lamniformes, Rajiformes, Rhinobatiformes e Pristiformes, com as raias afetando negativamente as taxas de extinção dos Lamniformes. Essa competição intraclado pode estar associada com similaridades ecológicas (estratégias de captura de presas) ou devido a habitarem o mesmo ambiente;
- Também foi observada competição entre Orectolobiformes e Squaliformes, com esse segundo sendo influenciado pelo primeiro. Neste caso, a competição possivelmente

está associada com similaridades filogenéticas, uma vez que essas duas ordens são filogeneticamente próximas;

- A diversificação de Delphinidae aumentou as taxas de extinção dos Hexanchiformes, Myliobatiformes e Squaliformes, provavelmente devido a similaridades morfológicas (corpo em formato fusiforme), similaridades ecológicas (todos os grupos são considerados macropredadores) ou por habitarem os mesmos oceanos.
- O esfriamento do planeta pode ter tornado os membros da familia Delphinidae um grupo fortemente competitivo frente aos Neoselachii ectotérmicos.

Nossas análises encontram evidências de que os fatores abióticos e bióticos influenciaram negativamente as taxas de extinção dos Neoselachii. Os resultados aqui apresentados podem ser úteis em estudos de predições futuras. Por serem um grupo pouco estudado e fortemente ameaçado de extinção, faz-se necessárias mais estudos para que políticas de conservação sejam implementadas a fim de mitigar os danos causados pelo aquecimento global e suas consequencias nas mudanças das interações ecológicas.

AGRADECIMENTOS

Agradeço à CAPES, FAPITEC e CNPq pelo suporte financeiro para o desenvolvimento deste projeto.